

Nearly Optimal Foraging in Patches Under Nutrient Constraints

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Abstract. Three feeding strategies with different rules for prey selectivity were evaluated by Monte Carlo computer simulation. The predator must obtain a minimum quantity of each of three different nutrients, and it sequentially encounters one of three kinds of prey that differ in both their nutrient compositions and their relative abundances. Within patches, prey may be randomly dispersed or aggregated with Markovian transition probabilities. Overall cost is the sum of search time plus consumption cost plus emigration (between-patch traverses) risk. The predator will emigrate if it is unsuccessful in acquiring a minimum of Γ units of any needed nutrient within the T most recent prey encounters. The three strategies are (1) no discrimination—with potentially high consumption costs, (2) minimal consumption—with potentially very prolonged search times, and (3) a hybrid strategy that requires a physiological monitoring of net nutrient acquisition (or the bookkeeping of highly correlated gustatory cues). Each strategy has its characteristic dynamics and optima, but collectively these simulations show that no one strategy is superior and that over a large portion of the parameter space the differences in overall cost are relatively small.

Introduction

This study uses computer simulation to examine the consequences of different consumption (or foraging) rules when a predator must obtain a minimum amount of three different nutrients from prey that differ in their nutrient composition and their abundance. Two basic questions are addressed: (1) What kinds of decision rules are useful for a predator with a nutrient-constrained diet, and how

robust are these rules over the parameter space of the model? (2) When prey are distributed in patches (in which one kind of prey predominates), what foraging strategy and which decision rules for leaving nonproductive patches are superior?

This general model can be used for many species of predator, but a particularly apposite example is that of an omnivorous intertidal gastropod, moving randomly over rocks with encrusting or sessile prey in an area where, because of both accident and microgeographic variation, one rock is colonized chiefly by barnacles, another by algae, yet another by mussels, and so on. If individual prey are refractory (like barnacles), the consumption costs may be substantial compared to the search costs. The gastropod emigrates by releasing its hold on the substrate and allowing wave action to redeposit it at some distance from the previous site; here the main cost of emigration could be exposure to predation and the risk that no suitable site whatsoever is found, but these costs can be converted into the currency of "time" commensurate with the search and consumption costs. The omnivorous feeding of intertidal gastropods has been extensively studied (see Largen, 1967, and Vadas *et al.*, 1994, on the dogwhelk, *Nucella* [= *Thais*]; Menge, 1974, on *Acanthina*; Wood, 1968, on the oyster drill, *Urosalpinx*), although direct evidence for nutrient-constrained diets in these species is sparse. However, Speiser and Rowell-Rahier (1993) have found prey selectivity in a helcid snail, *Arionta*, a terrestrial relative of intertidal gastropods which shares their proverbial locomotion rates.

In my simulations, the search for suitable prey is a stochastic process (Oaten, 1977; Green, 1987)—hence replication is necessary to evaluate the different factors in the experimental design. This model is intended to be simple but general: simple in that there is no satiation, no contests or competition for resources, and the predator

encounters prospective prey as a consequence of simple Markovian transition probabilities. The model is general in that there are three dietary constraints with three kinds of prey, and two parameters for prey distribution (relative abundance and spatial aggregation).

In the past 20 years, many papers on foraging strategies have been published, and it is not possible to review them all. Pyke *et al.* (1977), Pyke (1984), and Real and Caraco (1986) are good overviews; Pulliam (1974, 1975) succinctly introduces the key points addressed here; and see the Discussion. Many of the recent papers have been based on field studies, which augment the earlier theoretical and laboratory investigations. However, a survey of the literature shows that studies of nutrient-constrained diets seemingly are under-represented (Westoby, 1978; Belovsky, 1990). There are probably two main reasons for this. First, for many species, nutrient considerations are not important—the predator may be essentially monophagous, or if not, it may fulfill all its nutritional needs by serendipitously consuming prey with complementary nutrients without requiring specific adaptations for prey discrimination. Second, it is much more difficult to assay an array of nutrient compositions within prey species and then to demonstrate that the differences in acquisition rates of these nutrients have significant physiological effects on a predator than it is to measure total calories consumed or tabulate search and handling times.

Methods and Experimental Design

In all the simulations described here, there are three nutrients and the forager is required to obtain a minimum amount [MR] of each kind. There are three species, Prey1, Prey2, and Prey3, and every individual of each species has the same total number of nutrient units summed over the three kinds, but the experimental parameter, ξ , determines the composition of the nutrients within each species. Thus we have a **nutrient matrix**, where K designates the mean nutrient level per individual in arbitrary units—in all the simulations the three nutrients are scaled to this common factor:

	Nutrient1	Nutrient2	Nutrient3
Prey1	$(1 + \xi)K$	K	$(1 - \xi)K$
Prey2	$(1 - \xi)K$	$(1 + \xi)K$	K
Prey3	K	$(1 - \xi)K$	$(1 + \xi)K$

The range of ξ is from 0 (all prey have K units of each nutrient) to 1 (each prey type has $2K$ units of one nutrient, and K and 0 of the other two). We also permit ξ to have negative values in the range of 0 to -1 , and this specifies the following matrix:

	Nutrient1	Nutrient2	Nutrient3
Prey1	$(1 + 2 \xi)K$	$(1 - \xi)K$	$(1 - \xi)K$
Prey2	$(1 - \xi)K$	$(1 + 2 \xi)K$	$(1 - \xi)K$
Prey3	$(1 - \xi)K$	$(1 - \xi)K$	$(1 + 2 \xi)K$

This matrix produces a greater nutrient disparity, with the limit of $3K$, 0, 0 units for $\xi = -1$, but as in the first case all the rows and columns sum to the same value ($3K$).

In these simulations $K = 8$ and the minimum requirement [MR] is 240 units of each kind (the scaling is arbitrary). It is clear that for any value of ξ (positive or negative), the required 240 units of each of Nutrient1, Nutrient2, and Nutrient3 can be met if exactly 10 items of each prey type are consumed (*i.e.*, $[10][3K] = 240$), and this total of 30 prey consumed is a minimum value as well (designated N_{\min}). It therefore follows that even with large nutrient disparities ($|\xi|$ near 1), if the abundances of the three prey are nearly equal, the forager can expect to fulfill its nutritional requirements without an extended search (though it would be very lucky indeed to find exactly 10 prey of each type in the first 30 random encounters). If one prey species is much more abundant than the other two, the predator faces a greater challenge. For all values of $|\xi| < 1$, it is clear that an exclusive diet of any one prey type can provide the required amount of all three nutrients, but for $|\xi|$ near 1, a large number of prey must be eaten (*e.g.*, if $\xi = +0.9$ or -0.9 , then 300 of the one prey must be eaten). On the other hand, the predator may consume only the minimal number of prey—10 of each type—but if one prey type is rare, then the forager may require very long search times to find the 10 rare prey.

The within-patch abundance distributions are constructed analogously to the nutrient matrices, with δ determining the relative abundance as follows: For $\delta > 0$, $\text{Prey}_C = 0.333(1 + \delta)$; $\text{Prey}_I = 0.333$; $\text{Prey}_R = 0.333(1 - \delta)$. For $\delta < 0$, $\text{Prey}_C = 0.333(1 + 2|\delta|)$; $\text{Prey}_I = 0.333(1 - |\delta|)$; $\text{Prey}_R = 0.333(1 - |\delta|)$. The subscripts C, I, R indicate the common, intermediate and rare prey types within a given patch, with three kinds of patches ($\text{prey}_C = \text{Prey1}$ or Prey2 or Prey3) represented equally. Thus the overall abundance (for any value of δ) of each prey type over the entire ensemble of patches is 0.333. For example, if $\delta = +0.6$, then in one-third of the patches $\text{Prey1} = 53\%$, $\text{Prey2} = 33\%$, and $\text{Prey3} = 13\%$; in another third, $\text{Prey1} = 13\%$, $\text{Prey2} = 53\%$, and $\text{Prey3} = 33\%$; in the remaining third, $\text{Prey1} = 33\%$, $\text{prey2} = 13\%$, and $\text{Prey3} = 53\%$.

These two experimental parameters, ξ and δ , may be varied independently (see Appendix A), but abundance disparity is of no consequence (costs will always be minimal) if all the prey types are nutritionally equivalent (ξ

= 0). With equal abundances ($\delta = 0$ so all $p_i = 1/3$) and marked nutrient disparities, costs will usually be close to minimal as well, but stochastic variation in encounters will occasionally engender markedly higher costs. (This situation would be reversed of course, if the nutrient compositions were random variables and the prey encounters were strictly deterministic.) Therefore, to avoid the proliferation of experimental treatments, the two parameters are usually varied as pairs, with $\xi = \delta = D$ (the disparity index), with $-0.9 \leq D \leq +0.9$.

Studies on intertidal species, as well as many other field studies, have shown that in nature species are usually not distributed independently, but tend to be clumped or aggregated. (More rarely, prey may be overdispersed, but this is a beneficial situation for foragers with incompletely substitutable resources.) If the prey are distributed independently, then random encounters may be simulated by repeatedly generating a pseudo-random variable uniformly distributed on the interval [0,1] and by designating the prey type encountered in conformance to the within-patch abundances $[p_1, p_2, p_3]$. For aggregated prey, the encounter procedure employs the first-order Markov process defined by the following matrix:

	Prey _{1,t+1}	Prey _{2,t+1}	Prey _{3,t+1}
Prey _{1,t}	$(p_1 + R - 1)/R$	p_2/R	p_3/R
Prey _{2,t}	p_1/R	$(p_2 + R - 1)/R$	p_3/R
Prey _{3,t}	p_1/R	p_2/R	$(p_3 + R - 1)/R$

This matrix specifies the probabilities for encountering Prey_j at time $t + 1$ given that Prey_i had been encountered at time t , where R is the **aggregation index**. If $R = 1$ then all rows reduce to the independent trials vector, $[p_1, p_2, p_3]$, but as R increases, the diagonal entries increase and the other probabilities decrease, which of course means that successive encounters of the same prey type become increasingly likely—in other words, the prey are clumped. Regardless of which prey type is initially encountered upon entering a patch, if the predator remains within a patch for a sufficiently long time, the proportion of encounters converges to the vector of the independent trials process.

What kinds of decisions might a forager make when faced with incompletely substitutable resources? First, within a patch, there are two *unconditional* strategies: the forager can either (1) eat every prey item that it encounters—the TAKE-ALL strategy or (2) eat only the minimum number of prey (10 of each)—the SELECTIVE strategy. There is a cost associated with both finding the prey (**search costs**) and capturing, ingesting, and otherwise handling the prey that the forager decides to pursue and consume (**consumption costs**). Hence the objective of the model forager is to minimize the time needed to find

and consume enough prey to meet the prescribed nutrient vector.

In addition to deciding whether or not to eat a particular prey item, the predator has the option of leaving one patch (for which the abundant prey species is no longer a desirable item of diet) for another (with the hope that, in the new patch, the abundant prey will provide a needed nutrient). Emigration also entails a cost (**traversal cost**), and it is further assumed that the new patch cannot be selectively chosen (*i.e.*, the three kinds of patches are equally likely, and therefore one-third of the time the forager will emigrate to a patch like the one just abandoned).

In the general model, the environment consists of many patches with each of the three prey types being most abundant in one-third of them, so that overall the prey and nutrient availability is concordant with the dietary requirements. In each simulation, all patches have the same disparity indices [$\xi = \delta = D$] and aggregation parameter, R . The predator does not change from its initial strategy, so that the single-patch simulations are the special case of multiple-patch foraging in which the emigration rule is "remain in original patch." What sort of emigration rules might a predator employ? Because emigration costs (or traverse times) are higher than either search or consumption costs, a reasonable rule would delay emigration as long as the current patch is assessed as "productive" by some criterion. Emigration decisions in previous studies as well as this one are almost always based on the following general principle (Charnov, 1976; Oaten, 1977; Regelman, 1986; Valone, 1992): the predator is able to monitor its foraging success, and when its gain fails to attain a minimum level (in many models this is caused by depletion of limited resources) the predator leaves for potentially more productive regions (or switches to an initially inferior prey). A fundamental premise of these experiments is that the predator's sensory system can monitor the gain of each of the three needed nutrients. This model uses two parameters, T and Γ , for the emigration algorithm that is employed by all strategies: *Remain in the current patch if at least Γ units of any needed nutrient have been acquired over the last T encounters, otherwise emigrate.*

This model assumes that each patch is large relative to the predator's search area and that the search is conducted over previously unexplored territory; in other words, the prey are not depleted.

A final consideration is how to weight the three kinds of incurred costs. If search costs are large compared with consumption costs, the decision is simple: the TAKE-ALL tactic is superior; if traversal costs are small and the prey aggregated but very disparate in their nutrient composition, then the best strategy is to emigrate as soon as the

forager is confronted with superfluous prey. The most interesting case is where Search Cost (β_S) < Consumption Costs (β_C) < Traversal Cost (β_T). For the general case, the search cost is 1 in arbitrary "time" units and the other two costs are arbitrary multiples of this unit, but this entails a two-dimensional parameter space for the weighting function. To simplify the experimental design, the following assignments are used:

Cost Parameter:	β_S	β_C	β_T
LOW	1	2	4
MEDIUM	1	3	9
HIGH	1	5	25

Cost = β_S (prey encountered) + β_C (prey consumed) + β_T (patches traversed).

The complete model includes all the parameters mentioned above—all applicable to each consumption rule—and this implies a seven-dimensional space generated by the vector [$\delta, \xi, R, \Gamma, T, \beta_C, \beta_T$]; even if the computational limitations were not a factor, it would not be possible to visualize the results for the fully realized model.

In all experiments, the number of replications is 100 (see Appendix B).

Results

Single-patch foraging without aggregation

Although the stochastic results are central to this study, it is useful to begin by comparing the deterministic and stochastic (independent trials) costs, the former serving as a baseline. In the deterministic case, the prey are encountered and consumed within each small time interval in direct proportion to their abundance. The number of prey consumed by a "deterministic" TAKE-ALL predator confined to a single patch is, when both δ and ξ are positive and both are equal to D, equal to

$$\frac{N_{\min}}{1 - \frac{2D^2}{3}} \quad (1)$$

When either or both δ and ξ have negative values, the deterministic consumption costs are the same. For the case where $|\delta| = |\xi| = \text{eq } D$, the total prey consumed is

$$N_{\min}/(1 - D^2) \quad (2)$$

For example, if $\delta = \xi = 0.9$, then 66 prey must be eaten [$30/(1 - 2(0.81)/3) = (30/(0.46))$]. For those cases

where either δ or ξ or both = -0.9 , 159 prey ($30/(1 - 0.81)$) are required—a more than fivefold increase over N_{\min} .

A forager in stochastic environments where $\delta = 0.9$ and $\xi = -0.9$ consumes an average of 162 prey (*cf.* 159 above), whereas if both parameters = -0.9 , the average rises to 186 prey. Although a predator will occasionally do better with stochastic encounters than with deterministic encounters, over the long run the latter has lower mean costs. A comparison of the stochastic and deterministic case for TAKE-ALL foraging over all combinations $\delta, \xi = \pm 0.3, \pm 0.5, \pm 0.7$, and ± 0.9 showed that the number of prey eaten in the stochastic case is greater by 12% (both $\delta, \xi > 0$), 9% ($\delta > 0; \xi < 0$), 6% ($\delta < 0; \xi > 0$) and 29% (both $\delta, \xi < 0$) than in the corresponding deterministic case.

The SELECTIVE predator always consumes $N_{\min} = 30$ prey but for any pair of δ and ξ , it must encounter more prey than the TAKE-ALL predator, with much larger numbers for extreme disparities. For example, for $D = -0.9$, the average number of prey encountered is 354, a more than tenfold increase over N_{\min} . High consumption costs favor the SELECTIVE tactic and low consumption costs favor the TAKE-ALL strategy.

For deterministic encounters where $\delta = \xi = D < 1$, the SELECTIVE (abbreviated SEL) predator encounters $N_{\min}/(1 - |D|)$ prey and consumes N_{\min} prey. The TAKE-ALL (abbreviated T-A) predator encounters and consumes $N_{\min}/(1 - |D|^2)$ prey. For both, Cost = $C_S + C_C = \beta_S \times$ prey encountered + $\beta_C \times$ prey consumed, and with $\beta_S = 1$:

$$\text{Cost}_{\text{SEL}} = N_{\min}[1/(1 - |D|) + \beta_C] \quad (3)$$

$$\text{Cost}_{\text{T-A}} = N_{\min}[(1 + \beta_C)/(1 - |D|^2)] \quad (4)$$

These costs are the same for the trivial case, $D = 0$, but the two expressions are otherwise quite different. However, in this specific case, the "cross-over" value for β_C , designated β_C^* (for $\beta_C < \beta_C^*$, $\text{Cost}_{\text{T-A}} < \text{Cost}_{\text{SEL}}$; for $\beta_C > \beta_C^*$, $\text{Cost}_{\text{T-A}} > \text{Cost}_{\text{SEL}}$) is

$$\beta_C^* = 1/|D| \quad (5)$$

This simple relation is unexpected because for other combinations of δ and ξ the algebraic expressions are messy. This concise result is partially deceptive, however, for although it shows that for values of D near zero, the TAKE-ALL strategy is superior to the SELECTIVE strategy over a wide range of β_C , a graph of the costs of the two strategies versus β_C (Eqs. 3 and 4) for small D shows that the two lines are nearly coincident, and therefore the superiority of TAKE-ALL is inconsequential (because both kinds of predator encounter and consume close to N_{\min}

prey). What is important is the converse conclusion: if D is greater than 0.5, then *SELECTIVE* will be superior whenever β_c is greater than 2, and for even larger disparity values, the *SELECTIVE* strategy will always be preferred unless the consumption cost is almost as low as the search cost.

Over a range from moderate to extreme disparities in nutrient composition and abundance and with different levels of the Cost parameter, there is no single optimal consumption [*TAKE-ALL* vs. *SELECTIVE*] strategy. For any particular prey and predator species, the nutrient disparity (ξ) among the different prey is likely to be relatively invariant over ecological time, and consumption costs will usually be nearly constant. But certainly the prey abundances $|\delta|$ can vary widely (in this sense perhaps β_c rather than β_s should be fixed in the experimental design, but the distinction is arbitrary; moreover, β_c can encompass secondary considerations such as increased predation risk while eating—which would not necessarily be constant over all localities).

Because either the *SELECTIVE* or *TAKE-ALL* rules can incur very high costs depending on δ and ξ and the relative search and consumption costs, these experiments include a third strategy that might reduce the risk of large costs by being a hybrid between the *TAKE-ALL* and *SELECTIVE* rules. This hybrid is the *THRESHOLD* strategy whereby the predator initially adopts a *TAKE-ALL* strategy but, once it has acquired a *threshold* amount of a specific nutrient, it will no longer eat the prey type which is highest in that nutrient. Usually the threshold value is set to $1.25 \cdot MR$. If it were equal to MR (240 units), this third strategy would resemble closely—but not be identical to—the *SELECTIVE* strategy; if much higher, it would resemble the *TAKE-ALL* strategy. An extensive analysis of the deterministic case is not warranted, but to illustrate the analytical impediments, the deterministic expression for the *THRESHOLD* (abbreviated *THR*) strategy where the threshold = MR and $\delta = \xi = D < 0$ (the simplest case algebraically!) is

Prey encountered

$$= N_{\min} \left\{ \frac{8D^2 - |D| + 2}{(1 - |D|)(1 + 2D^2)(2 + |D|)} \right\} \quad (6a)$$

Prey consumed = $N_{\min} \left\{ \frac{6D^2 + |D| + 2}{(1 + 2D^2)(2 + |D|)} \right\} \quad (6b)$

Figure 1 displays the results of the stochastic simulations for the three strategies where $\delta = \xi = D = \pm 0.3, \pm 0.6, \text{ and } \pm 0.9$ with Cost Parameter = Medium ($\beta_c = 3$). Also shown are the average costs for the 5% most-costly replications (*i.e.*, the "worst 5%" of the 100 repli-

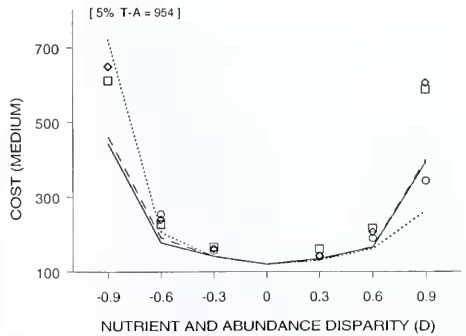


Figure 1. Costs incurred over different prey abundances and nutrient compositions (D) by the three strategies in stochastic single-patch foraging. The lines (dotted = *TAKE-ALL*; solid = *SELECTIVE*; dashed = *THRESHOLD*) connect the mean costs of 10 independent simulations each comprising 100 replicates. The symbols (circles = *TAKE-ALL*; squares = *SELECTIVE*; diamonds = *THRESHOLD*) designate the average of the costs incurred by the 5 replicates with the highest costs ("High 5%").

cations). Clearly, there is no unconditionally superior strategy.

Prey aggregation

In the analysis above the prey are encountered as an independent trials process; the aggregation parameter, R , alters the probabilities of the transition matrix. Although the stationary vector of the Markov process is the same as the independent trials process, Figure 2 illustrates that clumping with $R = 2$ or $R = 4$ increases the search times with the greatest effect on the *SELECTIVE* and *THRESHOLD* predator. A more detailed comparison between *TAKE-ALL* and *SELECTIVE* is given in Table I; the first entry within each cell is the average cost for the *TAKE-ALL* simulations and the second for *SELECTIVE* simulations. These data show that increasing R has a larger effect on the *SELECTIVE* predator.

Higher R values increase the costs for the single-patch simulations because the greater number of successive encounters with the abundant prey delays the needed acquisition of the scarce nutrients. The mean run-length for prey is equal to $1/(1 - \pi_u)$ where the π_u are the diagonal elements of the transition matrix. The mean run-length for the most abundant prey ($i = c$) within a patch (L_c) is, for $\delta > 0$:

(Distribution I) $L_c = \frac{3R}{2 - |\delta|}$ and, for $\delta < 0$, (7)

(Distribution II) $L_c = \frac{3R}{2(1 - |\delta|)}$ (8)

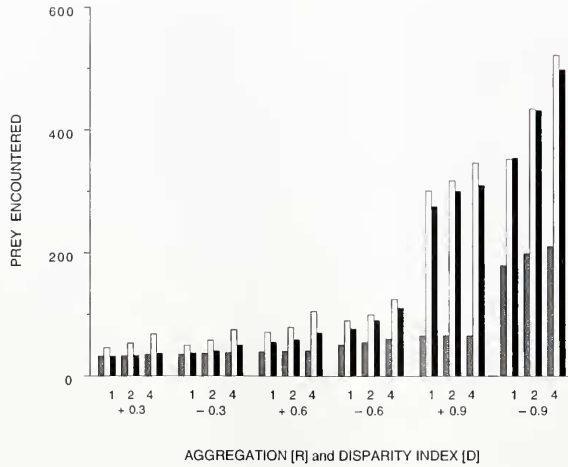


Figure 2. Mean number of prey encountered by predators adopting one of three strategies for single-patch foraging. The data for the different aggregation indices, R, equal to 1, 2, or 4, are nested within the different disparity indices, D = ±0.3, ±0.6, and ±0.9. Hatched bars = TAKE-ALL; open bars = SELECTIVE; solid bars = THRESHOLD.

For the rarest prey, for both Distribution I and II,

$$L_R = \frac{3R}{2 + |\delta|} \tag{9}$$

Because $|\delta| < 1$, we have the corresponding ranges for L_C and L_R :

I: $1.5 R \leq L_C < 3 R$ II: $1.5 R \leq L_C < \infty$

I, II: $R < L_R \leq 1.5 R$

From the above inequalities, it is apparent that (a) for any

π_n , the average run length is proportional to R, which can be arbitrarily large; (b) for a given R, the value of δ has little effect on L_R ; and (c) δ has only a modest effect on L_C for Distribution I, but for Distribution II, L_C will attain very high values if $|\delta|$ is near 1 even if R is not especially large. And of course, high values for L_C mean a "long wait" for the scarce prey type.

To encapsulate the results for the single-patch case, I tabulated the costs incurred by the three strategies over 9 combinations of the aggregation index (R = 1, 2, and 4) and Cost parameter (Low, Medium, and High) crossed

Table I

Single-patch foraging: Comparison of TAKE-ALL and SELECTIVE strategies over three values of R and six values of the disparity index, D (n = 100 for all simulations)

D	Cost Parameter = LOW				Cost Parameter = HIGH				
	R:	1	2	4	Best	1	2	4	Best
+0.3		98 < 106	100 ≈ 114	104 < 128	T-A	195 ≈ 196	199 ≈ 204	208 < 218	T-A
-0.3		106 ≈ 110	110 < 118	115 < 135	T-A	212 > 200	220 > 208	229 ≈ 225	SEL
+0.6		119 < 132	122 < 140	124 < 165	T-A	238 > 222	245 > 230	249 ≈ 255	SEL
-0.6		154 ≈ 150	165 ≈ 160	182 ≈ 185	—	307 > 240	329 > 250	367 > 275	SEL
+0.9		197 < 361	198 < 378	196 < 407	T-A	395 < 451	395 < 468	392 < 497	T-A
-0.9		540 > 414	598 > 495	644 > 582	SEL	1080 > 504	1195 > 585	1268 > 672	SEL

For each comparison, the TAKE-ALL costs are on the left and the SELECTIVE costs are on the right; the Best column indicates the strategy with the lower (or equal) cost for all values of R.

with 6 values of the disparity index, D , giving 56 comparisons. I also included another 27 "worst case" comparisons [using the means of the 5 most costly replications for each strategy] over $D = -0.6, +0.9, -0.9$ and the three R values and the three Cost indices as above. For each comparison, a tie was declared if the average costs of the greatest and least of the three strategies differed by less than 3% (see Appendix B), and if the extremes of the "High 5%" differed by less than 6%.

	Lowest Cost (best strategy)			Highest Cost (worst strategy)		
	Mean	High 5%	Total	Mean	High 5%	Total
TAKE-ALL	18	17	35	17	8	25
SELECTIVE	20	6	26	8	9	17
THRESHOLD	1	3	4	14	9	23

Of the 83 comparisons, the results of 65 are tabulated above; the other 18 were "3-way ties." TAKE-ALL was either the best or the worst in 60 out of the 65 non-tied comparisons. THRESHOLD was in the middle most frequently (59%) and has the lowest best-to-worst ratio (4 "bests" to 23 "worsts").

Multiple-patch foraging

The results for multiple-patch foraging are summarized in Figure 3, constructed analogously to Figure 1. No single pair of values for the emigration parameters (here $\Gamma = 8, T = 4$) can be optimal over all strategies and disparities, but these are "middle-of-the-road" values. A comparison of Figures 1 and 3 clearly shows that when emi-

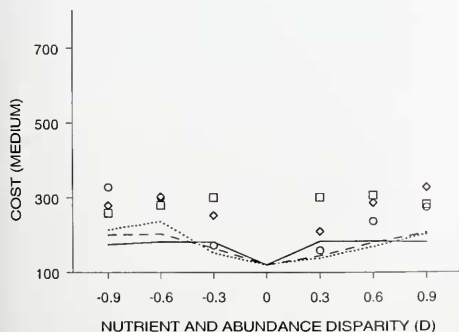


Figure 3. Costs incurred by multiple-patch foragers with $\Gamma = 8, T = 4$; symbols and other parameters—including the 10 repetitions—same as in Figure 1.

gration costs are three times greater than consumption costs (and nine times greater than search costs), for values of $|D|$ greater than 0.3, a predator (of any kind) will almost always reduce costs by emigrating.

Because each new patch is chosen as an independent trials process with probability = 0.333, it is easy to show that an average of 4.5 emigrations is required for a predator (of any kind) to visit all three kinds of patches; this is then the optimal number of emigrations for $D < 0$ given that multiple-patch foraging is superior to single-patch. For $D > 0$, emigration to either kind of patch different from the initial patch should suffice, since only one nutrient will be strictly limiting; this requires on the average 1.5 emigrations.

The value of T specifies the physiological memory window, and at one extreme, the emigration decision is determined entirely by the predator's success with the last prey item. For $T = 1$, Γ values of 2 and 8 produced essentially the same emigration rates for both SELECTIVE and THRESHOLD predators; their means are

	$D = +0.6$	-0.6	$+0.9$	-0.9
SELECTIVE:	12.6	11.3	12.6	6.6
THRESHOLD:	5.2	7.8	12.3	7.1

As a consequence of these high emigration rates, the non-emigrant predators had lower costs (both Low and High) except at the highest D values. TAKE-ALL predators tended to remain in the original patch when $\Gamma = 2$, but emigrated when $\Gamma = 8$ (as tabulated below):

TAKE-ALL:	3.0	8.0	3.4	6.6
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All these average emigration rates are higher than the "optimal" values of 1.5 (for $D > 0$) and 4.5 (for $D < 0$).

Table II shows the effect of varying both T (from 1 to 8) and Γ (from 2 to 16) so that all experiments monitor the same rate of nutrient gain (2 units per time interval). The main entries are total cost [Cost Parameter = Medium; $R = 1$] associated with the different pairs of Γ and T . The last row gives the averages over all three strategies and disparities; this is instructive in showing that collectively the differences across the spectrum of short-term ($\Gamma = 2, T = 1$) to longer term ($\Gamma = 16, T = 8$) assessment are not large. Note that greatest and least costs for any strategy are not distributed consistently over either rows or columns, and in a few cases the differences are sizable.

Figure 4 shows the average number of emigrations for each strategy over two values of Γ (4, 16), two values of R (1, 4), and four values of D ($\pm 0.6, \pm 0.9$), where $T = 4$. Note that there is a cluster of points for emigration values from 10 to 12; as was the case for $T = 1$, all

Table II

Mean costs (Cost parameter = Medium; $R = 1$) for different emigration parameters (Γ , T) and disparity indices (D)

Strategy	Emigration Parameters [Γ , T]			
	2, 1	4, 2	8, 4	16, 8
D = +0.6				
TAKE-ALL	(160)	(162)	(159)	(160)
SELECTIVE	253	199	178	192
THRESHOLD	195	190	180	189
D = -0.6				
TAKE-ALL	(205)	(207)	(206)	(207)
SELECTIVE	226	188	187	191
THRESHOLD	224	217	208	201
D = +0.9				
TAKE-ALL	204	199	216	232
SELECTIVE	243	201	187	206
THRESHOLD	282	228	217	224
D = -0.9				
TAKE-ALL	208	211	218	261
SELECTIVE	195	174	176	186
THRESHOLD	209	199	207	211
Average:	217	198	195	205

Values in parentheses are simulations in which the predator *always* remained in its initial patch.

three strategies are susceptible to "over-emigration" with consequent increased costs. The outlier is a TAKE-ALL predator that remains in its initial patch because it always obtains at least 4 units of needed nutrient in four encounters.

Table III provides a comprehensive overview of the effect of different Γ values on emigration rates. Note the following points.

1. There are marked differences in the pattern and number of emigrations among the three strategies when viewed as a whole; the average number of emigrations (not including the values for $\Gamma = 32$, which is clearly too stringent a criterion) are TAKE-ALL = 0.84; SELECTIVE = 5.55; THRESHOLD = 3.16.

2. For SELECTIVE and THRESHOLD predators, values of Γ of 1, 2, 4, or 8 usually produce similar emigration rates within each strategy.

3. The aggregation index, R , has only a small influence on the number of emigrations, and the sign of D affects the number in an inconsistent way. For the SELECTIVE and

THRESHOLD predators, the Table III data, excluding those for $\Gamma = 32$, can be synoptically tabulated:

	Average Number of Emigrations				
	SELECTIVE		THRESHOLD		
	D > 0	D < 0	D > 0	D < 0	
R = 1	5.3	4.8	R = 1	2.9	3.2
R = 4	6.5	5.5	R = 4	2.9	3.7

When prey have the more exclusionary nutrient composition ($\xi < 0$), the average number of emigrations is less for the SELECTIVE predator than when the prey are more "substitutable"; the reverse is true for the THRESHOLD predator. The average number of emigrations from Table III for TAKE-ALL ($R = 1$ and $R = 4$ combined) are 0.4 for $D > 0$ and 1.2 for $D < 0$. These are significantly less than the "optimal migration rates" of 1.5 and 4.5, but if only emigrants are averaged, the rates are close to optimal.

4. The SELECTIVE predator has uniformly high emigration rates for all entries with $D = +0.3$ and -0.3 , which represent a quite modest disparity in both abundance and nutrient content

Other considerations

How sensitive is the THRESHOLD strategy to the value of the coefficient that determines the nutritional limits? All simulations reported above used a threshold coefficient of 1.25, and Table IV summarizes the results for other values with $R = 1$, and averages taken over $D = \pm 0.3$, ± 0.6 , ± 0.9 . There is less than a 4% difference in the average costs for the three different coefficients (1.05, 1.25, and 1.5) in both single- and multiple-patch simulations, so its precise value does not seem an important consideration. The simulations employing large values of 2.0 and 5.0 are interesting but extreme; as noted, the data in these columns show congruence to the TAKE-ALL model.

Another consideration is whether one strategy might entail extreme costs more often than another strategy, even when they have similar average costs; many have argued that a predator should choose a strategy that avoids extreme values rather than an alternative that might have significantly lower *average* costs but is more susceptible to occasional runs of bad luck that engender ruinously high costs (Caraco, 1980; Houston and McNamara, 1985; Real and Caraco, 1986; Weissberg, 1991). In Figure 5, the average costs (of all 100 replications) of the three strategies are plotted against the average of the five replicates with the highest costs ("High 5%"). There are six

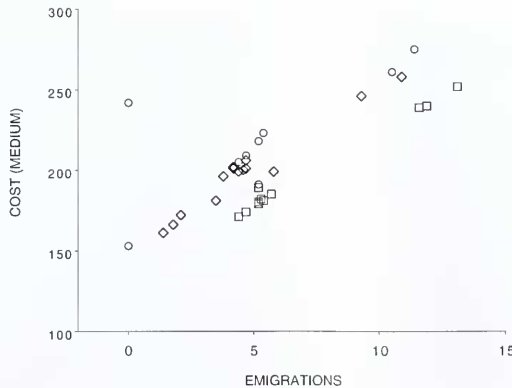


Figure 4. Mean number of emigrations versus average costs for three strategies (symbols same as Figures 1, 3).

points (all for single-patch foragers) that are off-scale; their values and their ratios (5% mean/overall mean) are TAKE-ALL: 490/283 = 1.73, 1200/877 = 1.37; SELECTIVE: 1185/425 = 2.79, 1495/639 = 2.34; and THRESHOLD: 1384/455 = 3.04, 1347/640 = 2.10.

This effect is also seen if the high 5% are substituted for the bottom row ($D = -0.9$) values of Table I that show uniform superiority of SELECTIVE over TAKE-ALL; the values with (*) are exceptions to this pattern.

Cost Parameter	R = 1	R = 2	R = 4
Low	718 > 572	851 < 890*	900 < 1465*
Medium	957 > 602	1135 > 920	1200 < 1495*
High	1435 > 662	1702 > 990	1800 > 1555

These reversals are caused by the higher variances in the SELECTIVE strategy over TAKE-ALL (with THRESHOLD being intermediate). From Tables B1 and B2, the average CVs are

	TAKE-ALL	SELECTIVE	THRESHOLD
single patch:	1.03	1.34	1.18
multiple patch:	1.61	2.04	1.74

The TAKE-ALL strategy has the lowest variance because the predator will always gain some needed nutrient at every encounter, no matter how unfavorably the prey are distributed.

Discussion

Applicability of model

Demonstrating that nutrient constraints are important in shaping feeding patterns is difficult, especially because

there are other reasons for prey selectivity (Westoby, 1978; Speiser and Rowell-Rahier, 1993; Ball, 1994; Vadas *et al.*, 1994; Brown and Morgan, 1995). Nonetheless, there are a number of field studies that support the contention that differences in nutrient composition among prey have ecological and evolutionary significance (Belovsky, 1978 [moose, *Alces*]; Clark, 1980 [feral rat, *Rattus*]; Calvert, 1985 [gorilla, *Gorilla*]; Karasov, 1985 [ground squirrel, *Ammospermophilus*]; Thomson *et al.*, 1987 [junco, *Junco*]; Ritchie, 1988 [ground squirrel, *Spermophilus*]; Wallis de Vries and Schippers, 1994 [cattle, *Bos*]; Forchhammer and Boomsma, 1995 [muskoen, *Ovibos*]; Kennish, 1996 [crab, *Grapsus*]; see also Waldbauer and Friedman, 1991 [various insects] and Rapport, 1980 [ciliate protozoan, *Stentor*]).

How relevant are the results of these simulations to the interpretation of such field studies, and how limiting are the assumptions of the models employed? Is this model realistic in requiring a maximum of only three nutrients, in its parameterization of the prey distribution, and in its assumption that a forager can monitor its nutrient acquisition?

1. A comprehensive model of nutrient-constrained foraging should normally require no more than three nutrients (and therefore no more than three prey). More than three nutrients may be desirable in a diet, but deficiencies in the additional nutrients are unlikely to produce strong selective pressures. I could find no evidence that a species in the wild is constrained by more than three nutrients. Calvert (1985) measured 11 constituents in 27 species of plants eaten by the mountain gorilla and found that only three components (lignin, fiber, and protein) determined prey selectivity.

Table III

Average number of emigrations for different values of Γ for $T = 4$ over 6 values of the disparity index, D

D =		+0.3	-0.3	+0.6	-0.6	+0.9	-0.9	+0.3	-0.3	+0.6	-0.6	+0.9	-0.9	+0.3	-0.3	+0.6	-0.6	+0.9	-0.9
Γ	R	TAKE-ALL						SELECTIVE						THRESHOLD					
		32	1	1.5	4.3	4.8	10.1	7.7	11.3	16.1	19.6	17.6	13.3	20.2	12.1	1.4	4.8	5.3	9.6
	4	1.9	5.2	3.3	10.5	5.7	11.4	21.6	21.6	20.0	13.1	21.8	11.9	2.1	5.4	4.1	11.0	6.0	10.5
16	1	0	0	0.5	4.3	2.5	4.4	6.2	8.7	11.1	5.6	12.2	4.6	0	1.0	4.3	4.4	2.0	4.4
	4	0	0	1.1	4.4	2.4	4.7	11.9	11.6	10.8	5.2	11.2	4.7	0.7	3.5	6.2	4.5	7.0	4.6
8	1	0	0	0	0	1.6	4.4	3.4	2.9	5.1	5.0	4.8	4.5	0	0.4	2.0	3.9	5.0	4.7
	4	0	0	0	0	1.7	5.2	5.6	5.7	5.1	5.2	6.3	5.2	0.6	2.1	3.1	4.2	4.1	4.7
4	1	0	0	0	0	1.6	4.6	2.2	3.6	5.2	5.2	5.0	4.6	0	0.3	2.6	5.0	4.4	4.7
	4	0	0	0	0	1.6	5.4	4.8	5.3	5.0	5.4	5.2	5.3	0.4	1.4	2.5	4.7	4.1	4.6
2	1	0	0	0	0	0	0	3.1	3.2	5.3	5.4	4.5	4.7	0	0.2	2.7	4.6	4.3	4.6
	4	0	0	0	0	0	0	5.3	5.3	5.3	5.2	5.1	4.4	0.6	1.8	2.3	3.8	4.0	4.7
1	1	0	0	0	0	0	0	2.6	3.3	4.8	5.4	4.8	4.8	0	0.4	2.1	4.1	4.5	4.4
	4	0	0	0	0	0	0	5.5	4.8	5.0	5.2	6.0	4.6	0.6	2.2	3.0	3.9	4.1	5.2

2. Many prey species may have more than two levels of spatial distribution and abundance, but the slight gain in realism achieved by incorporating a third level would be offset by increased complexity in the experimental design (see Underwood and Chapman, 1996).

3. The nutrient (ξ) and abundance (δ) disparity parameters were subsumed under one disparity parameter, D , and Appendix A considers the consequences of reducing the parameter-space. All nutrients and prey types have the same values in this symmetric model (240 units of each nutrient can be obtained from 10 prey of each type). But these are essentially relative values; the same general conclusions would obtain if different nutrients had differ-

ent minimum requirements and if prey differed in size. Obviously this model loses relevance for extreme departures from this idealized situation—for example, the case where eating a single individual of one kind of prey sufficed for one nutrient, and several hundreds of smaller individuals of a second kind of prey were needed for a second nutrient. If applied to a specific field study, this model could incorporate additional parameters reflecting the particular physiology and ecology of the predator.

4. To an observer, the TAKE-ALL predator behaves within a patch as if it were not subject to any nutrient constraint, and the only evidence that it is monitoring nutrient gain would be its sporadic emigration. In this sense, the TAKE-ALL rule serves as a control to which the SELECTIVE and THRESHOLD strategies may be compared. The simulations assume that the THRESHOLD (and the TAKE-ALL) foragers can monitor nutrient acquisition, whereas the SELECTIVE predators are presumed to have an instinctive prey selectivity shaped by experience over evolutionary time. If individual prey differ in size (or for other reasons differ in nutrient content), SELECTIVE predators, going strictly by the numbers of prey consumed, will be more likely to have nutrient deficiencies than will the predators that can assess nutrient gain. For the THRESHOLD predator, what is the biological justification for the threshold coefficient (here 1.25), which may be either (1) a value crafted by adaptation to allow for imprecision in assessment or inherent variability in nutrient requirements, or (2) a parameter reflecting the time lag between the time of ingestion and the physiological processing of food's nutrient composition (so that some "overshoot" inevitably occurs)? Although nutrient gains usually cannot be assessed immediately in terms of physiological benefit, it is plausible that a species might evolve

Table IV

THRESHOLD strategy with different threshold-limit coefficients: all entries are averages over six values of the Disparity index [$D = \pm 0.3, \pm 0.6, \text{ and } \pm 0.9$]; aggregation index (R) = 1

	THRESHOLD Coefficient				
	1.05	1.25	1.50	2.00	5.00
Single-Patch ($\Gamma = 0$)					
Average prey consumed	34.0	36.1	38.3	41.6 ^a	50.0 ^b
Mean cost [medium]	256	247	249	240	242
$\Gamma = 8, T = 4$					
Average prey consumed	34.0	36.5	39.2	43.4 ^a	56.5 ^b
Average emigrations	3.4	2.8	2.3	1.6 ^c	0.07 ^b
Mean cost [medium]	178	181	184	193	235

^a For both single-patch and $\Gamma = 8, T = 4$, THRESHOLD was equivalent to TAKE-ALL for $D = \pm 0.3$ and $+0.6$.

^b THRESHOLD same as TAKE-ALL for all D except $D = -0.9$.

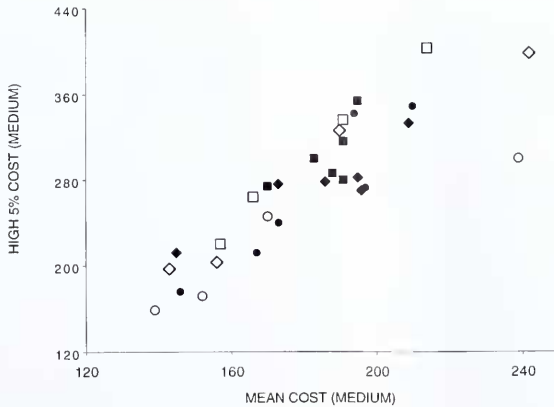


Figure 5. Mean costs versus "High 5%" for the three strategies. $R = 4$; $\Gamma = 8$; $T = 4$. Symbols same as Figures 1, 3, with open symbols = single-patch and solid symbols = multiple-patch. $D = \pm 0.3, \pm 0.6$, and ± 0.9 (multiple-patch only).

the capability to monitor nutrient intake more promptly but indirectly by relying on correlated gustatory or olfactory cues.

In light of the above contention, it is helpful to summarize a series of laboratory experiments performed over a number of years using rats subjected to suboptimal diets. Richter *et al.* (1938) showed that laboratory rats given the opportunity to select from a variety of foods (olive oil, casein, sucrose, cod liver oil, wheat germ oil, yeast, and four inorganic salts—all supplied in excess) had the same weight-gain, longevity, and fecundity as those raised on the best commercial diets, while actually consuming a lower total weight of food. In the authors' words, the rats had a "special appetite not only for salt and sugar, but for protein, carbohydrate, sodium, calcium, phosphorus, potassium and . . . [vitamins]." Morrison (1974) demonstrated that well-fed rats typically demonstrated a preference for novelty in their diets, even for substances that ranked very low in palatability (as ranked in prior studies in which alternatives were supplied *ad libitum*).

Rodgers and Rozin (1966) demonstrated that thiamine-deficient rats sought novelty in their diets at a higher level than nondeficient rats, even though previous dichotomous choice experiments had shown that thiamine-deficient rats were unable to detect (or at least did not prefer) a thiamine-supplemented diet item over one lacking in thiamine. Rodgers (1967) concluded that "there are a rather large number of needed vitamins and minerals, and it is unreasonable to attribute to the animal the ability to recognize the taste or smell of all of these, as would be required if all specific hungers [his term for prey selectiv-

ity] were unlearned." Consequently, his diet-choice experiments suggest that an inherent bias for novelty in the diet is enhanced when animals are lacking in one or more important nutritional components.

Rozin (1969) has postulated that the preference for novelty is actually an aversion to the food previously consumed, which the rat perceives as being responsible for its decline in vigor. His results corroborated earlier work on rats with vitamin B-complex deficiencies. Harris *et al.* (1933) showed that rats could not detect which one of six foods contained the necessary vitamin supplement, but characteristically ate one or two different alternatives on successive days, with all six eventually being consumed in roughly the same amounts. They concluded that "the ability of the vitamin B-depleted rat to discriminate between diets containing the vitamin and those deficient in it depends not on vague instinct but on an association between the distinctive character of the diet . . . and an experience of prompt beneficial gains . . . which follow immediately [!] on its consumption."

5. This model does not take into account predator satiation, prey depletion, or time constraints (Stephens and Krebs, 1986; Brown and Mitchell, 1989; Ward, 1993b). Satiation imposes an upper limit on a TAKE-ALL predator, and time constraints would limit the number of prey encounters for SELECTIVE and THRESHOLD. A satiated TAKE-ALL predator is likely to behave like a THRESHOLD predator; a SELECTIVE (or THRESHOLD) predator will probably become less discriminating if its foraging time is frequently restricted by extrinsic factors. Species typically subjected to rigorous environmental fluctuations may

have to substitute local [sub]optimal solutions for the globally optimal one (Ward, 1993a, b); his example is oystercatchers, whose prey show intertidal zonation and therefore prey choice is adversely curtailed by tidal cycles. Prey depletion within patches can be accommodated within this model because rate of nutrient gain will necessarily decrease as prey are depleted, triggering emigration as specified by T and Γ (see Brown and Mitchell, 1989; Mitchell, 1990). In sum, the limitations of this model are ones suggested by common sense. If a TAKE-ALL predator typically consumes between 35 and 50 prey, it is unlikely that it could eat 150 to 200 or more prey within a comparable time period when faced with an extremely disadvantageous prey distribution. In this case the outcomes might be reduced fitness, or reversion to an escape behavior such as diapause or migration, or a change in feeding strategy (the TAKE-ALL predator imitates a SELECTIVE one). It is also reasonable to suppose that a SELECTIVE predator, despite its instinct to eat a fixed [small] number of prey, would eventually eat previously rejected prey after extended searches failed to find the few rare prey that minimized consumption costs.

Conclusions

These simulations show that the three foraging strategies are relatively insensitive to variation in T and Γ (Tables II and III), provided neither value is very small or very large. However, the strategies have different optima for these values, and therefore each kind of predator would be likely to adopt different T and Γ values—since these are not fixed by the environment, unlike δ , ξ , and R (see Green, 1987). For example, a TAKE-ALL predator would be expected to employ a higher Γ value than a SELECTIVE one.

Both R and δ are likely to vary over an organism's feeding season and, more importantly, δ (and probably R) will be different in successive patches visited by each predator. These simulations had fixed (within an experiment) values for δ , ξ , and R , but overall the strategies were evaluated over a range of δ (as D) values. In the field, patch sizes will vary, but in this model prey are not depleted, so all patches are large relative to their diminution by consumption. Collectively, these simulations show that T , Γ are generally robust over a range of relative prey abundances; that is, a particular pair of values for T and Γ that are appropriate for habitats with high abundance disparities will adequately serve the predator in low-disparity environments.

The consequences of increased prey aggregation (higher R) are dichotomous: Figure 2 and Table I show that higher R values consistently increase costs for predators confined to just one patch, especially for SELECTIVE

foragers; with emigration, however, higher R values may shorten the time needed to acquire just the one needed prey. If very high R values are common, a species should decrease its memory window (T), thereby expediting emigration from patches that are no longer productive. As pointed out earlier, Table III shows relatively small effect of different R when $T = 4$; but when $T = 1$ ($\Gamma = 8$; Cost factor = Medium), a comparison of costs (over six values of D) for all three strategies reveals that the total costs for $R = 1$ are greater than for $R = 4$ in 15 cases, and are less in only 3. Moreover, a patch in which the prey have a low δ in conjunction with a large R may mimic a patch with much higher δ and no aggregation (independent encounters). Although there are exceptions, the general conclusion is that the deleterious effect of high R on single-patch foraging becomes a mild advantage for multiple-patch foraging.

There are two primary considerations in evaluating the different strategies. (1) How consistently does a strategy minimize costs within patches. (2) How robust is a strategy in keeping emigrations at a close-to-optimum number for given Γ , T over a range of environmentally determined values for δ , ξ , and R .

The quantitative results support the intuitive generalization that for all three strategies, predators should remain in the initial patch if all three prey are common, and should emigrate promptly from patches with high disparities once they have exploited the most abundant prey. The analysis may be extended by the following consideration: for any strategy with given δ , ξ , and β_T , the predator should either remain in the original patch and incur no traversal costs, or should emigrate to successive patches without modifying the emigration criteria, because the patch transition probabilities are independent of previous patches visited (see McNamara *et al.*, 1993). If emigration to a new patch has an expectation of lower overall costs than remaining in the original patch, then Γ and T should depend only on which strategy is employed, not the on values of δ and R . A predator is unlikely to find markedly different values of ξ from patch to patch (but nutrient compositions could vary over locality and season).

For single-patch foraging, with high D values and moderate to large search costs, SELECTIVE is superior to TAKE-ALL. The THRESHOLD strategy, although almost always second-best by a small margin to either SELECTIVE or TAKE-ALL, seems to be a workable compromise (see Figures 1 and 2).

For multiple-patch foraging, from an analysis of the cases for $D = +1.0$ or -1.0 , we can generalize to cases of intermediate disparities. Consider first the case for $D = -1.0$ (each patch is monotypic with completely exclusionary nutrient constitutions). The number of prey en-

countered and eaten for TAKE-ALL will be $30 + 4.5T$, and for SELECTIVE will be 30 eaten and $30.0 + 4.5T$ encountered. The THRESHOLD will be similar to TAKE-ALL. Emigration is a necessity and occurs promptly; the costs are therefore lower than for cases with intermediate values of D .

For the case in which $D = +1.0$, the predator needs to exploit only two different patches. The deterministic TAKE-ALL predator will encounter and eat $39.4 + 1.5T$ prey. The deterministic SELECTIVE predator will eat 30 prey while encountering $52.5 + 1.5T$ prey (and the THRESHOLD predator will be intermediate).

For negative D in Table III, the average number of emigrations is close to 4.5 as theory predicts, but for positive D , the values are usually higher than 1.5 . This is a consequence of the fact that even if the second patch is favorable (its most abundant prey is highest in the needed nutrient), there is a probability of $(2 - D)/6$ that the predator will initially encounter superfluous prey and then "mistakenly" emigrate from the patch.

When emigration is an option, for all three strategies over all combinations of parameters (including Γ and T), the total prey encountered is within the range of 30 to 48 . This is an important point that supports the conclusion that nearly optimal foraging can be obtained with more than one foraging rule. Consider two cases for multiple patch foraging:

I. Immediate Emigration ($T = 1$; $\Gamma = 8$; these values specify that the predator must emigrate if it fails to acquire at each encounter at least one needed nutrient at a rate equal to its average value over all prey types). These means are taken over all D (± 0.3 , ± 0.6 , ± 0.9):

TAKE-ALL: 43.9 eaten and encountered
 SELECTIVE: 30 eaten and 43 encountered
 THRESHOLD: 39 eaten and 44.5 encountered

The TAKE-ALL predator encounters more prey than does the SELECTIVE predator, but emigrates less often, which can offset the apparent inferiority of the TAKE-ALL strategy seen above (e.g., for $D = \pm 0.9$, the average number of emigrations is 5.0 for TAKE-ALL and 9.7 for SELECTIVE).

II. Moderate Time Window ($T = 4$): the means are taken over $\Gamma = 16, 8, 4$, and over all six values of D :

TAKE-ALL: 41.6 eaten and encountered (min = 32.5; max = 52.0)
 SELECTIVE: 30 eaten and 45.5 encountered (min = 39.5; max = 49.1)
 THRESHOLD: 36.5 eaten (min = 32.5; max = 39.5) and 45.7 encountered (min = 32.5; max = 55.5)

The minimum and maximum values for consumption and encounters are also indicated above. The THRESHOLD predator seems inferior to SELECTIVE, but the former has markedly lower average emigration rates (THRESHOLD = 3.2 ; SELECTIVE = 5.6).

The THRESHOLD strategy seems to be an effective and feasible (that is, biologically obtainable) tactic (Figs. 3, 4, and 5). The extent to which animals in the wild have adopted this "rarely optimal but often nearly optimal" strategy (see Real and Caraco, 1986; Ball, 1994; Ward, 1992, 1993a, b) remains an open question. Given the inherent stochasticity of the foraging process and the fact that throughout much of the parameter space the three foraging strategies dictate similar behavior, this question may be difficult to answer.

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Appendix A

In all the experiments, δ and ξ have the same value ($-0.9 \leq D \leq +0.9$). Although the nutrient and abundance matrices are mathematically equivalent, in the stochastic case, a given nutrient disparity is more costly to the predator than a comparable abundance disparity. For example,

Table A

The effect of different nutrient [ξ] and abundance [δ] disparities, $\Gamma = 8$; $T = 4$; the main entries are the means of (1) prey consumed, (2) prey encountered, and (3) emigrations

Strategy	$\delta, \xi =$		$\delta, \xi =$		$\delta, \xi =$		$\delta, \xi =$	
	+0.9,	+0.9	+0.9,	+0.9	-0.9,	-0.9	-0.9,	-0.9
	+0.9	+0.9	-0.9	-0.9	+0.9	+0.9	-0.9	-0.9
	R = 1							
TAKE-ALL	51, 51, 1.6	54, 54, 1.5	49, 49, 4.9	43, 43, 4.4				
SELECTIVE	30, 49, 4.5	30, 49, 5.0	30, 42, 4.7	30, 42, 4.5				
THRESHOLD	40, 56, 5.0	42, 54, 4.6	37, 56, 5.3	37, 50, 4.7				
	R = 4							
TAKE-ALL	47, 47, 1.7	53, 53, 1.5	44, 44, 5.5	43, 43, 5.2				
SELECTIVE	30, 45, 6.3	30, 42, 5.1	30, 43, 5.1	30, 42, 5.2				
THRESHOLD	39, 48, 4.7	41, 51, 4.2	36, 49, 4.9	37, 48, 4.7				

if $\delta = -0.3$ and $\xi = -0.7$, a TAKE-ALL predator (in a single patch) will consume 45.0 prey; if $\delta = -0.7$ and $\xi = -0.3$, then only 40.5 prey will be eaten.

In 24 such comparisons where $|\delta| \neq |\xi|$, 19 of these had greater costs when $|\xi| > |\delta|$, and the remaining five were ties. This general pattern also applies to the SELECTIVE and THRESHOLD predators. This is a consequence of the fact that if there is marked nutrient disparity but equal abundances, the predator is still subject to stochastic variation in encounters, whereas if abundances are disparate but prey are equivalent, there will be no deviation from the minimum number.

For multiple-patch foraging, Table A displays data for two additional cases, where $\delta = -\xi = \pm 0.9$. Overall, the data in the inner columns are similar to those in the outer columns for which $\delta = \xi = +0.9$ and $\delta = \xi = -0.9$. The small differences confirm that the nutrient disparity is more costly than an equivalent abundance disparity.

In conclusion, the restriction of the parameter space for spatial distribution and nutrient composition to those values of $\delta = \xi = \pm 0.3, \pm 0.6, \pm 0.9$ does not compromise the generality of the interpretations.

Appendix B

The data in this paper are averages of 100 replicate runs—each starting with a unique seed. Because of the variability from one replicate to another (which is the reason that the worst 5 of 100 replicates have much greater costs than the overall average), it is important to estimate the intrinsic variability between "runs." Tables B1 (for single-patch) and B2 (for multiple-patch) give the results of 10 repetitions of the " $n = 100$ " simulations.

These tables provide the basis for judging whether different parameter sets give significantly different results. The means (x) from the 10 replicate simulations have a t -distribution with 9 degrees of freedom, with standard deviation s . The 5% significance level for the difference of the means is equal to 2.2 (t with 18 degrees of freedom) times the s value: *i.e.*, if $x_1 - x_2$ is $> 2.2s$, then the means are significantly different. For most of the simulations, s is roughly proportional to the means; therefore, if two means differ by more than 3% (average CV approximately 1.2 for single-patch foraging) or 6% (average CV approximately 1.8 for multiple-patch foraging), the two costs are considered to be significantly different.

Table B1

SINGLE-PATCH: Means, standard deviations, and coefficients of variation (in %) of foraging costs (Cost parameter = Medium) for 10 replicate simulations, each consisting of 100 independent trials; $R = 1$

D	Sample*	TAKE-ALL			SELECTIVE			THRESHOLD		
		Mean	Std. dev.	CV	Mean	Std. dev.	CV	Mean	Std. dev.	CV
+0.6	All	161.0	1.49	0.93	165.3	2.91	1.76	166.6	1.43	0.86
	5%	188.8	3.39	1.80	215.5	5.82	2.70	209.7	5.23	2.49
-0.6	All	206.7	1.25	0.60	178.2	2.53	1.42	191.3	2.67	1.40
	5%	253.7	4.95	1.95	227.2	7.32	3.22	239.5	6.04	2.52
+0.9	All	263.8	4.54	1.72	392.7	6.41	1.63	400.0	7.12	1.78
	5%	342.5	7.76	2.27	588.0	16.34	2.78	604.8	15.84	2.62
-0.9	All	720.6	6.19	0.86	443.2	2.44	0.55	462.4	3.06	0.66
	5%	939.9	22.04	2.34	611.6	17.65	2.89	648.9	22.00	3.39

* All designates data for all 100 trials; 5% the data for the 5 "most costly" trials.

Table B2

MULTIPLE-PATCH: Means, standard deviations, and coefficients of variation (in %) of foraging costs (Cost parameter = Medium) for 10 replicate simulations, each consisting of 100 independent trials; $\Gamma = 8$; $T = 4$; $R = 4$

D	Sample*	TAKE-ALL			SELECTIVE			THRESHOLD		
		Mean	Std. dev.	CV	Mean	Std. dev.	CV	Mean	Std. dev.	CV
+0.6	All	169.1	3.11	1.84	183.5	6.15	3.35	179.5	3.81	2.12
	5%	236.9	9.04	3.82	307.0	27.81	9.06	286.0	11.78	4.12
-0.6	All	236.3	5.08	2.15	181.9	4.04	2.22	203.0	3.92	1.93
	5%	300.0	0	0	280.0	19.11	6.83	303.1	18.70	6.17
+0.9	All	202.6	1.90	0.94	180.8	2.44	1.35	207.0	3.50	1.69
	5%	274.0	11.35	4.14	281.9	14.75	5.23	328.3	22.93	6.98
-0.9	All	214.2	3.26	1.52	174.6	2.17	1.24	200.0	2.45	1.23
	5%	328.1	15.14	4.61	259.3	11.21	4.32	278.5	10.48	3.76

* All designates data for all 100 trials; 5% the data for the 5 "most costly" trials.